Forest Ecology and Management 261 (2011) 1936–1944

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Interannual variation in competitive interactions from natural and anthropogenic disturbances in a temperate forest tree species: Implications for ecological interpretation

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ARTICLE INFO

Article history:
Received 1 October 2010
Received in revised form 8 February 2011
Accepted 16 February 2011
Available online 10 March 2011

Keywords:
Acer saccharum
Competition–growth relationship
Ecological interpretation
Temporal variation
Disturbance
Light environment
Above-ground competition
Species coexistence

ABSTRACT

Competition is a major determinant of plant growth and is often used in studies of tree growth and species coexistence. However, these approaches are usually temporally static, i.e., assessed at a single point or period in time. While constantly changing forest conditions due to natural and human-induced disturbances potentially alter competition among individuals, static approaches cannot qualify the temporal variability of competitive interactions. Here we present a longitudinal analysis of competitive interactions among trees and discuss the implication of our results for ecological interpretation.

Spatially-explicit tree growth data were obtained from 18 study plots (0.4 ha each) in sugar maple (*Acer saccharum* Marsh.) stands in Quebec, Canada. During the studied period (1980–2003), these stands had been disturbed by insect outbreaks (forest tent caterpillar, *Malacosoma disstria* Hubner) and by commercial partial harvest. We analyzed radial growth rates (outcome of competition) on an annual basis and as a function of tree biology (bole diameter, crown position), competition (above- and belowground competition from neighbours) and environmental conditions (light availability, harvest disturbance).

Competitive interactions changed throughout the studied period. Canopy disturbance from partial harvest interacted with defoliators and influenced competition symmetry by favoring smaller trees.

Competitive interactions seemed to have switched from below- to above-ground following canopy recovery after harvest. Release from competition due to partial harvest increase neighbourhood size (radius of effective competition) and enhanced the competitive pressure from larger individuals.

The temporal variability in parameter estimates may be used for setting confidence intervals on competitive success (growth rates), thereby yielding a more robust basis for ecological interpretation. Our results also show that temporal variability in competitive interactions could contribute to the maintenance of high tree species diversity and structural complexity in some ecosystems by temporally altering species-specific responses to environmental change and disturbance.

1. Introduction

Plant growth is normally determined by the overall availability of resources and competition from neighbours that reduces their availability to any individual plant. Hence, competition has a direct influence on plant growth, and consequently, there is a rich body of literature on studies of plant growth using quantitative indices of intra- and interspecific competition, especially for trees (e.g., Bella, 1971; Hegyi, 1974; Daniels, 1976; Daniels et al., 1986; Holmes and Reed, 1991; Biging and Dobbertin, 1992, 1995; Canham et al., 2004; Stadt et al., 2007). Recent approaches have partitioned competitive effects of neighbours on tree growth into shading (above-ground) and crowding (below-ground or root) competition (e.g., Canham et al., 2004; Coates et al., 2009).

Competitive interactions have been used in explaining species coexistence and competitive displacement (e.g., Hara et al., 1995; Kubota and Hara, 1995; Nishimura et al., 2003) and some authors have used competition indices for that purpose (e.g., Canham et al., 2006; Uriarte et al., 2004a). Most of these studies, however, rely on an assessment of tree growth and competitive status at a single point in time without providing information on the temporal variability of the competition–growth relationship or how it varies as a function of changes in tree biological and environmental conditions (Wichmann, 2001). To our knowledge, only few studies aimed at quantifying a dynamic (temporally variable) competition index from tree-ring data analysis (Metsaranta and Lieffers, 2008; Weber et al., 2008).

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doi:10.1016/j.foreco.2011.02.018

Tree growth rates vary through time as a response to changes in environmental conditions (e.g., climate) and competition but also as a result of human or natural disturbances. These disturbances (e.g., partial harvests or insect outbreaks) selectively remove or kill neighbours from the competitive environment of residual (i.e., unharvested, surviving) trees and can therefore influence competitive interactions among individuals and the competition–growth relationship. Also, annual variation in climatic factors such as precipitation could, as Wichmann (2001) showed, change the symmetry of competition by giving larger trees competitive advantages in wetter years and thereby influence the competition–growth relationship.

To account for the temporal variability of tree growth rates some studies have modeled either time as a random effect (Fortin et al., 2008), estimated the temporal autocorrelation of growth rates (Kiernan et al., 2008) or computed the competitive status of trees retrospectively from spatially explicit long-term forest survey data (e.g., Canham et al., 2006; Papaik and Canham, 2006). However, there are, to our knowledge, no explicit studies of the temporal variability in the competition–growth relationship as a function of changes in forest conditions.

We used a 24 year chronology of sugar maple radial growth to investigate the influence of biological and environmental factors on temporal variation in the competition–growth relationship. Sugar maple (*Acer saccharum* Marsh.) is sensitive to drought and insect defoliation, which can cause forest decline and individual tree mortality (Kolb and McCormick, 1993; Payette et al., 1996). Regarding the latter disturbance, the forest tent caterpillar (FTC, *Malacosoma disstria* Hubner) causes severe reductions in radial growth, incurs branch and twig mortality, and weakens trees by exhausting carbon reserves through repeated defoliation (Wargo et al., 1972). This can render affected trees more susceptible to subsequent stresses such as drought (Renaud and Mauffette, 1991) or pathogens (Wargo and Houston, 1974), which in turn may reduce tree vigour and competitiveness.

Partial harvests likewise cause a redistribution of resources to residual trees, thereby causing a release from competition (Bevilacqua et al., 2005; Jones et al., 2009). However, the entry of heavy machinery (feller bunchers, cable skidders and forwarders) into forest stands during partial harvest may cause a combination of soil compaction and root damage to trees near skid trails (Kozlowski, 1999; Rönnberg, 2000; Nadezhdina et al., 2006). This disturbance may reduce water availability and uptake (Startsev and McNabb, 2001; Komatsu et al., 2007), and consequently, reduce the competitiveness of trees close to skid trails.

In our study we used multimodel inference (i.e., formal inference from more than one model) based on model averaging (i.e., weighted average of parameter estimates from all candidate models), to answer the following questions: (1) do changes in environmental conditions from insect defoliation, partial harvest, and climatic variation alter the competition–growth relationship in sugar maple and if so, (2) what are the implications for ecological interpretations of these competition–growth relationships?

2. Methods

2.1. Study sites

In 2004 and 2005, we established 18 plots (50 m × 80 m) in uneven-aged sugar maple stands in Quebec, Canada, about 60 km southeast of the city of Temiscaming (46°43′N, 79°04′W). Forests of this region are part of the western sugar maple-yellow birch bioclimatic domain, with a growing season of 170–180 days. Mean annual temperature varies from 2.5 to 5.0 °C and mean annual precipitation is about 900 mm, with ~25% as snowfall (Robitaille and Saucier, 1998).

Plots were located on level ground or on gentle slopes with good to moderate drainage. The soils were Ferro-Humic Podzols (Soil Classification Working Group, 1998), with underlying thin tills of glacial origin. The stands had been harvested in 1993 or 1994 by selection cuts, which removed ~30% of stand basal area (BA) with an average diameter of ~45 cm (±11 cm SD) at breast height. According to harvest regulations, tree selection aimed trees of low quality and vigour first and then high quality and vigorous trees (however, data on actual vigour of removed trees were not available). These were felled and lopped manually with chainsaws and the tree boles were forwarded to forest roads with cable skidders. Logging was done at various times during the year. Skid trail spacing was approximately 15 m, with some variation due to operational constraints. Selection harvest reduced average pre-harvest BA from 27 to 21 m^2/ha. In the post-harvest stands, sugar maple (Ms) constituted 74% of total BA, yellow birch (By, *Betula alleghaniensis* Britton) about 14%, American beech (Ba, *Fagus grandifolia* Ehrh.) roughly 4%, and balsam fir (Fb, *Abies balsamea* [L.] P. Mill.) 2.7%. White spruce (Sw, *Picea glauca* [Moench] Voss), red oak (Or, *Quercus rubra* L.), red maple (Mr, *Acer rubrum* L.), eastern hemlock (He, *Tsuga canadensis* [L.] Carr.), and eastern white cedar (Cw, *Thuja occidentalis* L.) constituted the remaining 5.3% of total BA. Sugar maple stands in the study region had also undergone several recurrent FTC defoliations over the last ~100 years, with the two most recent outbreaks occurring in 1986–92 and 1999–2002 (Hartmann and Messier, 2008).

2.2. Tree and skid trail mapping

In the 18 study plots, all live and standing dead trees ≥9.1 cm *DBH* (diameter at breast height, 1.3 m above ground) and all stumps from the most recent harvest were mapped. We mapped trees with a Hägloff Vertex III® hypsometer and a forester's compass and measured *DBH* of all live and dead trees and stump diameter at 0.5 m (DSH) of all trees harvested in 1993/1994. Trees were divided into four crown classes (*CROWN.POS*): dominant trees, the upper component of the main stand canopy, are characterised by well-developed crowns; co-dominant trees (C), the mid-component of the stand canopy, with less well developed crowns; intermediate trees (I), the lower component of the stand canopy, with crowns not directly exposed to sunlight; and suppressed trees (S), completely overtopped by the stand canopy. For snags (standing dead trees), we estimated time-since-death using three classes (0–5 years, 6–10 years, >10 years), based on external criteria such as the absence of bark and fine branches, stem wood decay, and crown deterioration (Sénécal et al., 2003) that are correlated with time since death. Skid trails of the 1993–94 harvests were identified retrospectively using presence of ruts, stumps, bole wounds, etc. (see Hartmann and Messier, 2008 for details) and then mapped based on tree positions within each plot using with an approximate 4 m average trail width.

2.3. Radial growth measurements

Within the 18 plots, we established subplots of 26 m × 56 m, in which we took three increment cores from all live sugar maple trees with *DBH* > 19.1 cm and <49.0 cm. Hence, sampled trees (n = 300) were surrounded by a 12-m buffer of mapped trees necessary for computations of neighbourhood competition indices (*NCI*, see below). Because the data were drawn from a study on mortality mechanisms in mature trees, only trees >19.1 cm and <49.0 cm were sampled during that time. This was to avoid heavily suppressed and especially senescent individuals. While data on trees beyond these bounds would have been useful for the purpose of the current study at least the exclusion of trees >49.0 cm in diame-

ter ascertains that competitive effects rather than intrinsic vigour decline was determinant for variation in growth rates.

Increment cores were progressively sanded to allow a clear identification of the final cell layer in each tree ring. In most cases, at least two of the three increment cores taken per live tree were readable and used for growth measurements. Tree rings were measured under a stereoscope equipped with a computer-assisted micrometer (0.001 mm precision). We obtained a single growth chronology per tree by averaging tree-level measurements, which accounted for intra-tree variability in radial increment due to growing conditions or leaning (Kienholz, 1930; Peterson and Peterson, 1995).

Among the resulting 300 sugar maple chronologies, we used those of dominant live trees to construct a master chronology. Using COFECHA software (Holmes, 1983; Grissino-Mayer, 2001) we progressively added highly correlated (e.g., *r*-values ≥0.3, Tardif et al., 2001) tree-ring series to the existing ones. The final master chronology comprised 29 trees and had an overall cross-correlation coefficient of 0.479. We cross-dated the remaining tree-ring chronologies by matching their growth rings with known calendar years of the master chronology, based on (1) visual examination of marker years (mainly severe growth declines in 1971 and 1988), and (2) cross-correlation coefficients of chronology segments with the master chronology. Missing or false rings within individual segments of tree-ring series were detected with the aid of COFECHA, and in suspect cases, were added (with zero growth) or removed from the series. Corrected series were then run again in COFECHA to verify the cross-correlation with the master chronology.

We used growth rates measurements only from 1980 onwards for further analysis because we assumed that the retrospective estimates of several predictor variables (e.g., *NCI*, *GLI*, see below) may not have been accurate beyond this point.

2.4. Neighbourhood competition index

We quantified competition experienced by tree *i* in neighbourhood *R* and at period *p* (see below) using several versions of the following *NCI* (Eq. (1)):

$$NCI_{ip} = \sum_{j=1}^{N} \frac{(DBH_j)^{\alpha}}{(dist_{ij})^{\beta}} \quad (1)$$

where DBH_j is the *DBH* of a neighbour tree *j* located at distance $dist_{ij}$ from subject tree *i*, for neighbours having a $DBH \geq 9.1$ cm. We considered all combinations of three α values (0, 1, or 2), four β values (0, 0.5, 1 or 2) and six *R* values (2, 4, 6, 8, 10 or 12 m). Hence, the *NCI* was either the count of competitors ($\alpha = 0$), the sum of competitor diameters ($\alpha = 1$) or the sum of their squared diameters ($\alpha = 2$) within radius *R* from the target tree. These values were either used as such ($\beta = 0$) or weighted by either the square-root of the distance ($\beta = 0.5$), the distance ($\beta = 1$), or the squared distance ($\beta = 2$) between the target tree *i* and competitor *j*. The minimum *R* value (2 m) was chosen to ascertain that at least one competitor would be theoretically present in the neighbourhood; the maximum radius (12 m) was set to be at least 3.5 times the estimated mean crown radius (2.7 m, estimated from stem diameter) in the study stands (Lorimer, 1983). We also tried several relative distances (e.g., height or 0.5 × height of target tree, radius proportional to the *DBH* of target tree) but with no improvement in model likelihood. Similarly we included species-specific competition indices in preliminary analyses to test for differences in sugar maple growth responses from intra- vs. interspecific competition but also with no improvement in model likelihood. Because sugar maple comprised ~68% of all trees we limited our analysis to a global (all species) *NCI*.

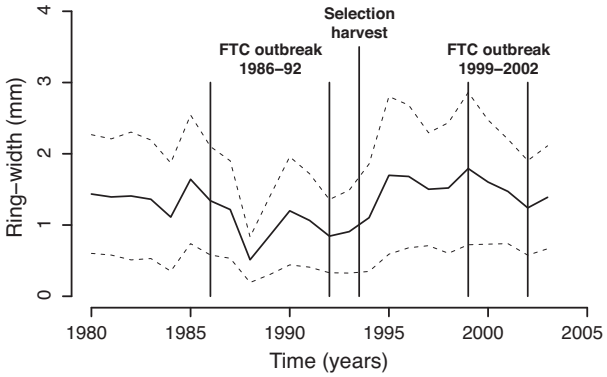

Fig. 1. Average (solid line) annual growth rates (mm/yr) of all sampled sugar maple trees ($n = 300$) and ±1 SD (dashed lines) from 1980 to 2003. Vertical lines indicate the periods of disturbance from partial (selection) harvest (1993–94) and FTC outbreaks in 1986–92 and 1999–2002.

We computed neighbourhood competition indices for three time periods *p*: (1) pre-harvest (1980–1993), (2) 0–5 yr post-harvest (1994–1998), and (3) 6–10 yr post-harvest (1999–2003). Pre-harvest *NCI* included harvested trees and trees that had died between harvest and sampling, 0–5-yr post-harvest *NCI* excluded harvest trees from these, and 6–10-yr post-harvest *NCI* additionally excluded trees that had died between harvest and 6–10 years after harvest. We computed *NCI* for $p = 1$ from data on live trees, stumps (location, DSH), and standing dead trees (location, *DBH*, estimated time-of-death) to reconstruct a map of competitors representing conditions prior to harvest. Standard conversion tables were used to estimate *DBH* from DSH (MRNFPQ, 2003). Because growth data was only available for target trees (and not for their competitors) we could not compute diameter distributions for prior periods and using average growth rates for estimations would only have yielded a linear shift in diameter distributions. However, the relatively small growth rates during the 24 year period (~1.3 mm average per year, Fig. 1) indicate that marked changes in competitive interactions from asymmetric shifts in diameter distributions during the studied period were unlikely in this forest community.

2.5. Estimation of light availability using SORTIE

Light availability for individual trees was estimated using the light module of SORTIE (v. 4.1), a spatially explicit individual-tree simulator of forest dynamics (Pacala et al., 1996). The SORTIE light module was parameterised based on species-specific allometric relationships and values of crown openness, which were estimated within the study region (Lefrançois et al., 2008) for sugar maple and yellow birch, the two most abundant species (89% of all trees in our plots). We used parameters from Canham et al. (1994), Beaudet et al. (2002), Beaudet (2004), and Poulin and Messier (2007) for other species present in the plot. In the rare cases where parameters were not available for a given species (4% of all trees), we substituted these with parameters from similar species (e.g., *Fraxinus americana* L. for *F. nigra* Marsh., Beaudet, 2004). We grouped standing dead trees into two classes (deciduous vs. conifers), and attributed a larger value of crown openness for these trees (Poulin and Messier, 2007).

We then loaded tree coordinates, *DBH*, and species identification of all live and standing dead trees into SORTIE to produce light estimates after significant stand changes as was done for NCI. Trees that were dead (but not felled) at the time of harvest and trees that died after harvest were included in the post-harvest stand maps as snags (conifer or deciduous) with corresponding crown openness values.

Light availability for each individual tree was estimated at height to live crown + 0.75 × crown length and represented the seasonally averaged percentage of full sun penetrating through the canopy (gap light index [*GLI*], Canham, 1988a).

2.6. Distance of trees to skid trails

Based on tree- and skid trail-maps and using GIS software (ArcGIS 9.2, ESRI, Redlands, CA), we computed the distance between a target tree and the closest skid trail (*DIST.TRAIL*) as a proxy for soil disturbance from machinery around target trees and as a measure of the potential influence of skid trails on target tree growth.

2.7. Summer temperature and rainfall indices as indicator of environmental condition

We used temperature and precipitation measurements from the two closest (~60 km) weather stations (Environment Canada, http://climate.weatheroffice.ec.gc.ca) and computed mean summer (April–August) temperature and rainfall from 1910 until 2003. We standardised these time series by dividing them by their respective averages and centred them on zero. This yielded summer temperature and rainfall indices that indicated annual proportional departures from the long-term average, where cold, dry summer conditions are associated with negative values and hot, wet summers with positive values.

2.8. Modeling radial growth as a function of competition, tree biological variables and changes in forest condition

Our modeling analysis was done in two steps to prevent model fitting of a very large number of models (and associated pitfalls, see Burnham and Anderson, 2002). The first step aimed at obtaining parameter estimates of the neighbourhood competition index for every time step (year) from 1980 to 2003. This was done by fitting several combinations of competition index parameter values to annual square-root transformed growth rates. Model averaging was employed to obtain annual NCI parameters estimates (alpha, beta, *R*; see Eq. (1)). The resulting neighbourhood competition index (*NCI*) was then used as a predictor in extended models (with alpha, beta, *R* now fixed). Again model averaging was used for parameter estimation of the extended models which included tree biological variables (*DBH*, crown position) and variables accounting for changes in forest condition (*DIST.TRAIL*, *GLI*, *NCI*).

2.8.1. Model averaging and multi-model inference

In model averaging, all models contribute to the parameter estimates and the predictions. Predictions of individual models are weighted based on the performance of a particular model among all candidate models and parameter estimates are averaged across all models containing the variable of interest. Model performance among all candidates is measured as Akaike weights derived from AIC_c values (Burnham and Anderson, 2002, see also Johnson and Omland (2004) for a very accessible treatment of model averaging and multi-model inference).

Model averaging also allows estimating unconditional confidence intervals (CI) of parameter estimates (Burnham and Anderson, 2002). These confidence intervals, estimated from the ensemble of models containing the term, were our criteria of parameter estimate 'significance' when a CI did not include zero. Goodness-of-fit of annual averaged model predictions was evaluated with a Pseudo-R^2 (ordinary R^2 is not defined for mixed-models), computed as the squared correlation between predicted (derived from model averaging) and observed values.

2.8.2. Estimating parameters of annual NCI-only models

We modeled annual radial growth rates as a function of competition (all possible functional forms of *NCI*) using a linear mixed-effect model (Eq. (2)):

$$Radial\,growth_{ikt}^{0.5} = \rho_0 + \rho_1 NCI_{ikp} + Zb_k + \varepsilon_{ik} \quad (2)$$

and $\varepsilon_{ik} \sim N(0, \sigma^2)$

The response variable, $Radial\ growth_{ik}$, was the (square-root transformed to homogenize variances) annual radial growth (in mm) of tree i in year t at site k (where sites correspond to the 18 sampled stands). NCI_{ikp} was one of all possible functional forms of the competition indices of tree i at site k with competitors accounted for when alive a period p. For this model, the ρ parameters were estimated as fixed effects and Zb_k as a random effect corresponding to random intercepts (one for each plot). The second variance component, the error term ε_{ik}, accounts for the intra-site variability. Both variances are assumed to be normally distributed with zero mean and variance σ^2 and model diagnostics did not indicate substantial departure from these assumptions. We estimated the parameters of the linear mixed effect models using the `lme` function from the `nlme` library (v.3.1-89, Pinheiro et al., 2008) in the `R` software (version 2.7.0, R Core development team 2008). Given that our analytic strategy included model averaging, we fit the models using maximum likelihood (Pinheiro and Bates, 2000). We evaluated model fit with AIC_c, an adjusted version of Akaike's Information Criterion (AIC) for small sample sizes (<40) per parameter estimated (Burnham and Anderson, 2002).

2.8.3. Extended models to account for competition, tree biological variables and changes in forest condition

To account for the fact that tree growth is not only determined by competition but also by tree biological variables as well as forest conditions, we extended the competition–growth model. We therefore estimated radial growth as a function of tree size, canopy position, light availability, disturbance from machinery traffic, and competition from neighbouring trees using linear mixed models. The global model had the following form (Eq. (3)):

$$Radial\,growth\,(mm)_{ikt}{}^{0.5} = \rho_0 + \rho_1 DBH_{ik} + \rho_2 CROWN.POS_{ik} + \rho_3 GLI_{ikp} + \rho_4 DIST.TRAIL_{ik} + \rho_5 NCI_{ikp} + Zb_k + \varepsilon_{ik} \quad (3)$$

$Radial\ growth_{ijt}$ was for tree i, site k, year t (1–24 yr), DBH_{ik} the tree diameter (mm) estimated at the time of sampling, $CROWN.POS_{ik}$ a categorical variable describing tree crown classes as defined in the tree mapping section and estimated at the time of sampling, GLI_{ikp} the measure of light availability (see section on light estimation), $DIST.TRAIL_{ik}$ the estimate of soil disturbance from skidding machinery traffic (for periods $p = 2$ and $p = 3$), and NCI_{ikp} was the measure of competition estimated for the three periods (as described above) with *NCI* parameters (R, α and β) obtained from model averaging in the previous step.

We estimated models of all combinations ($n = 31$) of the predictor variables *DBH*, *CROWN.POS*, *DIST.TRAIL*, *GLI*, and *NCI* (except for a trivial 'intercept only' model) for each calendar year. *DIST.TRAIL* did not enter the model in the pre-harvest period so there were fewer models during this period ($n = 15$). *GLI* and *NCI* computed for the pre-harvest period would enter the model in growth analyses for calendar years 1980–1993, 0–5-yr post-harvest *GLI* and *NCI* in calendar years 1994–1998, and 6–10-yr *GLI* and *NCI* in calendar years 1999–2003.

Table 1
Average count of competitors within a given search radius and average *GLI* (gap light index, i.e., seasonally averaged percentage of full sun penetrating through the canopy) of target trees before and after partial harvest and percentage change of inter-tree distances and *GLI* from partial harvest.

	Mean number of competitors		
Search radius (*R*, *m*)	Before harvest	After harvest	Change (%)
2	0.25	0.24	4.00
4	0.98	0.93	5.10
6	4.30	4.06	5.58
8	7.56	7.09	6.22
10	11.64	10.88	6.53
12	16.38	15.25	6.90
	GLI (%)		
	57.6	66.5	15.45

3. Results

3.1. Ring-width variation over time

Growth rates varied considerably among sampled trees. During the period 1980–2003, growth rates declined for almost all of the trees during the first FTC outbreak and attained their minimum in 1988 (Fig. 1). Average growth rates increased after partial harvest in 1993–94 and then decreased again during the 1999–2002 FTC outbreak (Fig. 1).

3.2. Changes in stand condition from partial harvest

Partial harvest reduced stand density and, by doing so, increased the average inter-tree distances between target trees and their competitors. Depending on the search radius, inter-tree distances increased by 0.81% (3.70 m to 3.73 m for $R = 6$ m) and up to 2.78% (1.08–1.11 m for $R = 2$ m) (Table 1). Average *GLI* increased by 15.45% from an average 57.6% (of available light) before harvest to 66.5% after harvest (Table 1).

3.3. NCI parameter approximation

Averaged *NCI* parameter values (R, α, β) showed substantial variation throughout the period (Fig. 2). In the years 1980 until 1995, the search radius R was on average 4.9 m but went above 6 m in 1980 (6.7), 1984 (6.4) and 1988 (6.2). From 1996 onwards, the R parameter was on average 7.8 m and > 8 m in 1997 (8.5), 2000 (8.6) and 2003 (8.3, Fig. 2). Parameter α oscillated around its 1980–2003 average (1.1) until 1996 and then increased to an average 1.5 in the 1996–2003 period. Similarly, parameter β was below its 1980–2003 average (0.5) until 1996 (0.4) and then increased (>0.6, Fig. 2).

3.4. Temperature and rainfall indices

The mean summer temperature was slightly below its long-term (1910–2003) average with an index value of 0.2. The coldest summer throughout the 1980–2003 occurred in 1992 (−0.100) and the hottest in 1998 (0.160). Mean summer precipitation was somewhat above its long-term average with an index of 0.077 and showed substantial variation during the 1980–2003 period (Fig. 2). Notable peaks occurred in 1980 (0.376), 1984 (0.531), 1988 (0.358) and in 1994 (0.302) and the driest summers were in 1982 (−0.164), 1989 (−0.164) and 2002 (−0.244) (Fig. 2).

3.5. Parameter estimates for predictor variables over time

Growth rates increased with tree diameter until three years after selection harvest (1996, except for 1991 and 1992) and then decreased until 2003 (Table 2). However, this relationship was significant only until the onset of the first FTC outbreak (1980–81, 1983, 1987), and then again, immediately before and during the second FTC outbreak (1998–2003, Table 2), which occurred in 1999–2002. Growth rates were highest for codominant trees (as indicated by negative parameter estimates for other crown classes) during the first FTC outbreak and before partial harvest, and higher than those of suppressed trees before and during the second FTC outbreak (Table 2).

Growth rates increased with distance from skid trails in 1997 and from 1999 until 2003 (Table 2). Increased light levels caused higher growth rates during the end of the first FTC outbreak (1989, 1991–92), in the years following partial harvest (1994, 1995) and then again during the end of the second FTC outbreak (2001, 2003) (Table 2). Competition (*NCI*) reduced growth rates in 1982 and 1990, in the years following partial (1996–97) and then again at the onset of the second FTC outbreak (1999–2000).

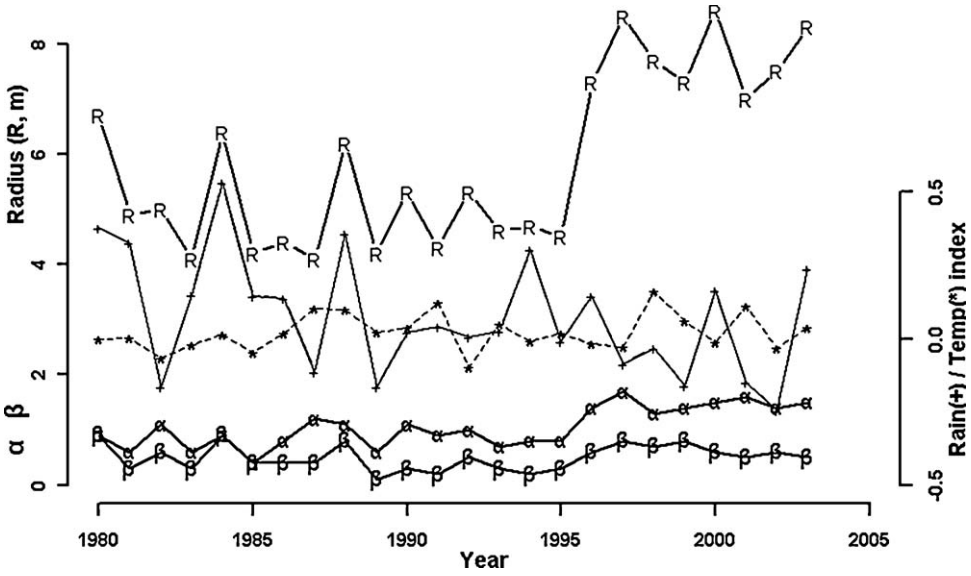

Fig. 2. Averaged *NCI* parameter values for search radius R (R), exponent α (α) of competitor *DBH* and exponent of distance between target tree and competitor β (β). Mean annual summer rainfall (+) and temperature (*) indices as proportional departures from average long-term (1910–2003) standardised summer (April–August) precipitation or temperature, respectively.

Table 2
Estimated mean annual radial growth obtained from model averaging and annual averaged parameter estimates (significant estimates, i.e., estimates whose confidence interval did not include zero are indicated with bold lettering) from mixed-effect modeling and for 1980–2003. Growth and parameters estimates were averaged based on Akaike weights derived from AIC_c values. Models with high AIC_c contributed less to growth and parameter estimates than models with low AIC_c. Shaded years indicate FTC defoliations (1986–92, 1999–2002). Partial harvest was conducted in 1993 (bold underlined line) and 1994. The distance to the nearest skid trail (*DIST.TRAIL*) entered models only after harvest.

	Mean annual	Predictor variables						
	Radial growth		*CROWN.POS*					
Year	Estimate (mm)	*DBH*	*S*	*I*	*D*	*DIST.TRAIL*	*GLI*	*NCI*
1980	1.352	**0.319**	−3.342	**−2.910**	**−3.585**		−0.001	−0.030
1981	1.320	**0.387**	−3.859	−2.372	**−3.328**		0.004	−0.139
1982	1.338	0.173	**−6.344**	**−4.075**	**−3.944**		−0.015	**−0.047**
1983	1.299	**0.295**	−0.827	−1.255	**−3.702**		0.026	−0.111
1984	1.034	0.009	**−4.783**	−1.982	**−3.018**		0.005	−0.041
1985	1.558	0.181	**−6.727**	**−4.394**	−2.898		0.018	−0.242
1986	1.272	0.168	**−6.378**	**−5.051**	−2.617		0.019	−0.066
1987	1.153	**0.170**	**−5.946**	**−3.876**	−2.670		0.022	−0.020
1988	0.484	0.029	**−3.984**	**−1.826**	**−2.376**		0.010	−0.006
1989	0.795	0.114	−2.540	**−3.727**	**−2.845**		**0.036**	−0.015
1990	1.119	0.046	−4.529	**−3.528**	−2.543		0.024	**−0.031**
1991	0.996	−0.010	**−5.090**	**−3.752**	**−2.640**		**0.042**	−0.005
1992	0.790	−0.005	**−4.573**	**−2.398**	**−2.978**		**0.035**	−0.017
1993	0.838	0.143	**−5.312**	**−3.876**	**−3.730**		0.032	−0.115
1994	1.011	0.074	−2.229	−2.240	−1.565	0.123	**0.049**	−0.064
1995	1.561	0.014	−5.422	−2.371	−1.551	0.139	**0.056**	−0.075
1996	1.564	−0.146	−5.606	−1.252	−2.386	0.177	0.023	**−0.019**
1997	1.414	−0.173	**−5.515**	−1.687	−2.930	**0.217**	0.013	**−0.008**
1998	1.409	**−0.334**	**−9.334**	−2.473	−3.398	0.224	0.034	−0.016
1999	1.652	**−0.249**	**−8.500**	−2.265	−2.221	**0.279**	0.025	**−0.018**
2000	1.509	**−0.228**	**−7.443**	−1.908	−1.704	**0.247**	0.036	**−0.013**
2001	1.395	**−0.212**	−4.178	−2.260	−2.315	**0.272**	**0.047**	−0.005
2002	1.167	**−0.340**	**−7.547**	−2.564	−2.250	**0.274**	0.034	−0.013
2003	1.305	**−0.360**	**−7.129**	−1.461	−1.331	**0.303**	**0.054**	−0.006

Note: DBH – diameter at breast height.
CROWN.POS – crown position within canopy (S: suppressed, I: intermediate, D: dominant), note that codominant trees represent the reference group.
DIST.TRAIL – distance from nearest skid trail.
GLI – light availability estimated as gap light index (see text for details).
NCI – neighbourhood competition index.

The contribution of predictor variables in predicting (square-root transformed) annual radial growth rates varied among years. In 1984–86, 1988 and 1993 only *CROWN.POS* was a significant predictor of radial growth whereas in 1994–95, only *GLI* and in 1996 only *NCI* was a significant predictor of growth rates. Never during the 24 year period were all predictors simultaneously significant. *DBH*, *CROWN.POS*, *GLI* and *NCI* had significant parameter estimates in 10, 20, 7 and 6 years, respectively, out of 24 years. *DIST.TRAIL* was a significant predictor variable in 6 out of the 10 years in the post-harvest period (Table 2).

Estimations of annual growth rates also showed considerable interannual variation. Lowest average growth rates were estimated in 1988 (0.484 mm) when the FTC outbreak was at its climax, while highest average growth rates were estimated for 1999 (1.652 mm, Table 2), more than three times higher than in 1988.

Averaged predictions from extended models generally confirmed superior model fit to the *NCI*-only models (Fig. 3). These models showed a best fit in 1983 with a peak in Pseudo-R^2 of 0.51 but then declined with several local peaks until 2003 to their lowest Pseudo-R^2 of 0.16 (Fig. 3). Similarly, averaged predictions from the extended models had a peak Pseudo-R^2 of 0.52 in 1983 and then declined to the lowest value of 0.20 in 2003 (Fig. 3).

4. Discussion

4.1. Do changes in environmental conditions from insect defoliation, partial harvest, and climatic variation alter the competition–growth relationship in sugar maple?

There was substantial interannual variation in the competition–growth relationship. Before partial harvest, positive *DBH* parameter estimates indicated that larger trees were able to secure proportionally more resources. This asymmetric competition pressure upon smaller trees, at least for above-ground resources such as light, translated into higher growth rates in larger trees (e.g., Schwinning and Weiner, 1998), but partial harvest presumably caused a redistribution of resources to fewer residual trees (Smith et al., 1997) and release of smaller

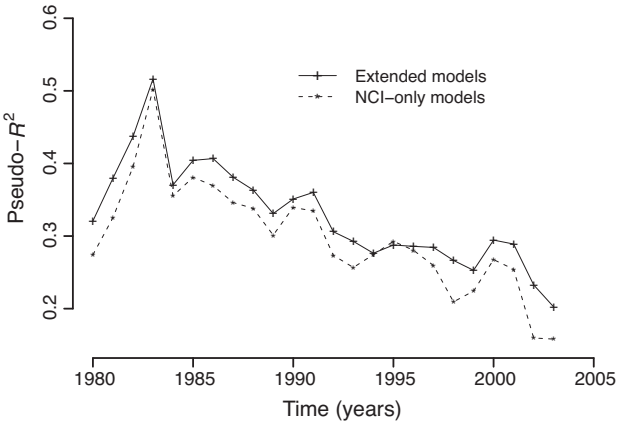

Fig. 3. Squared correlation coefficient (Pseudo-R^2) between observed and model-averaged predicted values as a measure of model fit of annual mixed models. Extended models contain all combinations of tree biological and environmental predictors (solid line, +) whereas *NCI*-only models (dashed line, *) predict growth rates from competition only.

trees from asymmetric competition. However, partial harvest did not cause suppressed trees to be permanently released from competition and their growth rates decreased again from 1997 onwards.

Negative parameter estimates for *DBH* in the post-harvest period may be explained by an interaction between partial harvest and FTC. Because larger trees have greater proportions of their canopy exposed to direct sunlight and because light-exposed leaves are the preferred food of FTC (Levesque et al., 2002), larger trees may have suffered proportionally greater defoliation than smaller trees. Hence, larger trees would have been most negatively affected by FTC, whereas the most suppressed trees, for which light availability (*GLI*) increased by 23–40% without, would have benefited the most from increased light levels from tree removal.

The positive effect of skid trail on radial growth after 1997, four years after partial harvest, may have been caused by increased water availability through reduced stand density (Bréda et al., 1995), once the negative effects of soil compaction and root damage were reduced (Malo and Messier, in press). Light availability (*GLI*) had a positive effect on tree growth in years following recovery from various canopy disturbances (FTC in 1988 and in 1999–2002 and partial harvest in 1993–94), possibly taking advantage of newly available growing space and securing light resources necessary for high growth rates (Canham, 1988b). The significance of *GLI* in the 1994–1995 period and subsequent significance of *NCI* in the period 1996–2000 suggests that there may have been a switch from above-ground (*GLI*) to below-ground competition (*NCI*) following the canopy recovery phase. However, because our study shares the uncertainty in the mechanistic basis for the crowding effects with other studies (e.g., Coates et al., 2009), we emphasize the need for caution when ecologically interpreting competition–growth relationships.

While neither our data nor our analytical approach allow an unambiguous identification of the causes for changes in *NCI* parameters, our empirical evidence (increases in effective competition radius, R, and in competitor size exponent α) indicates a release of close competition, as could be assumed for below-ground resources such as water (Schwinning and Weiner, 1998). Both calendar years 1984 and 1988 were wet years, which could have decreased competition for water. Increases in neighbourhood size following partial harvest may reflect decreases in plant competition for below-ground resources after gap creation (Cahill and Casper, 2002). The parallel increase of α with the increase in neighbourhood size corroborates this suggestion. After release of competition, only larger individual (as indicated by a higher α) may still contribute to resource competition (Schwinning and Weiner, 1998).

Declining Pseudo-R^2 values after the onset of the first FTC outbreak indicate that this change in forest condition was not appropriately accounted for by our predictor variables. In particular, our estimates of *GLI* were based only on average tree properties and locations (*DBH*, allometric relationship, crown openness, stands maps) but did not account for precise individual canopy condition. *GLI* is computed for individual trees as the seasonally averaged percentage of full sun penetrating through the canopy of their neighbours. Species-specific canopy openness parameters determine the degree of light extinction by neighbours but these parameters are estimated from trees with no signs of disease or senescence (Lefrançois et al., 2008). In reality, both FTC and selection logging would alter light availability for individual trees by introducing intra-specific variation in crown openness from selective feeding behaviour of FTC (Levesque et al., 2002) and, respectively, by intra- and interspecific variation of crown extension growth rates following disturbance (Runkle and Yetter, 1987).

There was considerable variation in both observed radial growth rates and in model predictions. Estimations of annual radial growth rates varied more than threefold between a good (1999) and a poor (1988) growing year (Table 2). Hence, growth predictions based on fixed competition indices that do not consider the dynamic changes in forest conditions could either over- or underestimate average growth rates, depending on the timing of parameter estimation. Moreover, our results highlight the need for more environmental information in competition-based growth models. Because of their influence on tree–tree interactions, climatic conditions (precipitation and temperature) and typical disturbance agents should be considered when growth is to be estimated from neighbourhood competition.

4.2. What are the implications for ecological interpretations of competition–growth relationships?

Recent studies in various forest ecosystems have shown that tree growth responses to crowding are both species and tree-size specific (Uriarte et al., 2004a,b; Coates et al., 2009). In this study, we show that these responses are not static through time due to both inter-annual variation in climatic conditions and natural or anthropogenic disturbances. These changing competition–growth relationships through time and following disturbances could also contribute in maintaining tree species diversity and structural complexity in species rich forest ecosystems. The tree-size dependent variation in growth response to disturbance found in our study should also favor structural differentiation over time in response to different disturbances.

Our results caution against ecological interpretations of neighbourhood sizes or of the functional forms of *NCI* with temporally static analytical approaches (e.g., Canham et al., 2004; Coates et al., 2009). We propose that such relationships should be quantified longitudinally by estimating parameters across periods of typical disturbance events for the forest ecosystem studied. The few studies in which temporal variation in growth rates was accounted for by either modeling time as a random effect, estimating the temporal autocorrelation of growth rates or the use of long-term forest survey data (e.g., Fortin et al., 2008; Kiernan et al., 2008; Canham et al., 2006; Papaik and Canham, 2006), do not alleviate this necessity because these methods do not explicitly characterize the temporal changes in the competition–growth relationship (but see Metsaranta and Lieffers, 2008; Weber et al., 2008). A statistical assessment of the temporal variability in parameter estimates would allow setting confidence intervals on growth estimates, particularly important when these are interpreted in terms of realized niches and species coexistence (e.g., Papaik and Canham, 2006; Coates et al., 2009).

In conclusion, our results highlight the need for caution when (1) estimating tree growth rates and (2) deriving ecological conclusions from tree biological and environmental conditions using temporally static neighbourhood analysis, i.e., competition indices that assume steady-state forest conditions. Our results may have major consequences on the conclusions of studies that make use of static analyses of competition–growth relationships in predicting temporally dynamic processes such as tree growth, survival or species diversity and coexistence but they could, on the other hand, also help explaining the high species diversity found in some forest ecosystems.

Acknowledgements

We would like to thank Catherine Malo for assistance in the field and laboratory (dendro), Bill Parsons for linguistic revision of the manuscript, Mélanie Desrochers for her support in GIS analy-

ses, and Denis Boileau and Louis Deschamps (MRNFQ) for logistical support. Financial support for this study was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) scholarship to HH, and a FQRNT (Fonds québécois de la recherche sur la nature et les technologies) grant to CM. We would also like to thank an anonymous reviewer for her comments on an earlier draft of the paper.

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